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Assessing the association between pathways of alien plant invaders and their impacts in protected areas

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Abstract

Protected areas face mounting pressures, including invasion by alien plant species. Scientifically sound information is required to advise invasive species management strategies, where early detection and rapid response is particularly important. One approach to this is to determine: (i) the relative importance of pathways of invasion by which a species is introduced, (ii) the range of likely impacts associated with each species, and (iii) the relationship between pathways and impacts, to assess the relative threats posed by different pathways of alien species introductions. This assessment was performed on 139 alien plants that are invasive across the South African National Parks (19 national parks, covering ~39,000 km^2), and based on available literature and expert opinion, known to have negative ecological impacts. For each species the likelihood of being introduced by each of eight pathways, and of having negative impacts in each of 13 identified impact categories, was assessed. The similarity of impact and pathway types between species was assessed using the Jaccard index and cladograms. Differences in the prevalence of impacts and pathways and relationships between these were assessed using a Chi-squared contingency and Generalised Linear Model. Nearly 80% of the species are ornamental plants and about 60% are also dispersed by rivers, highlighting the importance of managing ornamental species and surveillance along rivers in preventing future invasions. As to the impacts, ~95% of the species compete directly with native species and 70% change the physical structure of the environment. The majority of species exert multiple impacts, with 70% of species assessed having five or more impacts. There was a significant positive relationship between the number of pathways via which a species can be introduced into an area and the number of potential impacts they can have. This suggests that species using multiple pathways reach a wider range of suitable habitats, increasing the potential for different kinds of impacts over a wider area.

Keywords
Global change, Invasive alien plants, Management, Non-native species, Ornamental plants, State of knowledge assessment

Introduction

Protected areas represent some of the last opportunities to retain intact or at least relatively naturally functioning ecosystems with a near full complement of biological diversity (e.g. Geldmann et al. 2013). However, they are increasingly becoming disconnected remnants of natural habitats embedded within a larger mosaic of varying land use types (DeFries et al. 2005, Koh and Gardner 2010, Meiners and Pickett 2013). As such, these areas are threatened by a wide range of anthropogenic actions (Carey et al. 2000). One outcome of this is the mounting pressure of invasions by alien species from a multitude of different sources (Foxcroft et al. 2013, 2017, Hulme et al. 2013), each delivering different species and intensities of pressure (Pergl et al. 2016). Therefore an improved understanding of dispersal mechanisms is needed, to minimise not only possible future impacts (Pyšek et al. 2012), but also the costs associated with maintaining densities of alien plant populations below acceptable thresholds. Unfortunately, protected areas often have inadequate budgets for basic operational costs (Dixon and Sherman 1991, Bruner et al. 2004) let alone dealing with biological invasions (van Wilgen et al. 2016, Foxcroft et al. 2017). This necessitates careful prioritisation and allocation of funds to maximise long-term benefits (Leung et al. 2002, Evans et al. 2011, van Wilgen et al. 2016).

As with all conservation practices, the control of alien plant invasions requires scientifically sound information to advise policy strategies and management approaches (Cook et al. 2010). Although there is a rapidly expanding body of literature, this knowledge is often difficult to access and remains outside the realms of policy makers and managers (Cook et al. 2010, Sutherland et al. 2013). State of knowledge assessments are useful tools to examine scientific advancements and provide policy makers with information in a concise and usable form (e.g. prioritising species, pathways and sites, McGeoch et al. 2009).

Early detection, rapid response and eradication are regarded as the first line of defence in proactively managing alien plant invasions, and are considered wholly feasible in the protected area context (Simberloff 2013). However, the size and rapid escalation of the problem and the lack of adequate resources necessitates careful planning to ensure that management approaches are able to match the scale and rate of invasions and pre-empt future problems. Preventative strategies that have been developed either aim at assessing pathways or vectors of invasion, species-based prioritisation or prioritising sites (McGeoch et al. 2016). An assessment of possible introductory pathways can direct surveillance to enhance early detection strategies (Hulme 2006, Pergl et al. 2016). Additionally, the ability to predict or at least be aware of potential impacts is required to focus attention on the species already in the system most likely to be damaging to native species and basic ecosystem services (Kumschick et al. 2012). While various risk assessment approaches have been developed for pathway analysis (Dawson et al. 2009, Hulme 2009, Essl et al. 2015), many of these are aimed at preventing introductions at points of entry at a national scale, such as harbours and airports (see reviews by Hulme 2012 and Leung et al. 2012). However, at the scale of an individual protected area, local vectors need to be assessed.

Although conceptual frameworks for prioritisation based on potential impacts are evolving (e.g. Kumschick et al. 2012, Blackburn et al. 2014, Nentwig et al. 2016, 2018, Bacher et al. 2018) there is no single method that can be used in all contexts. A method developed to jointly inform prioritisation for management needs to include species, pathways, and susceptible or sensitive sites (McGeoch et al. 2016). Such a model provides a three-way prioritisation system which combines assessments of pathways associated with high-priority species, pathways of introduction to sensitive sites, and sites most susceptible to impacts of invasion by those same species (McGeoch et al. 2016). Protected areas with high biodiversity value are often delineated as susceptible or sensitive sites. However, between a set of parks, or the biomes in which they fall, there may be areas that are considered of higher importance (e.g. fynbos in Table Mountain National Park, Rebelo et al. 2011).

We used a combined assessment of the impacts that an invasive species can have and the potential pathways of invasion, to develop an approach to determine species of highest concern and inform management strategies. To do this we assessed 139 alien plants across the South African National Parks estate that are considered to be transformer or potential transformer species (i.e. the most invasive species) and determined: (i) the relative importance of pathways of invasion by which a species is introduced, (ii) the range of likely impacts associated with each species, and (iii) the relationship between pathways and impacts, to assess the relative threats posed by different pathways of alien species introductions in different parks and biomes.

Methods

Data compilation

We used South African National Parks (SANParks) as a model system as it has 752 alien plant species recorded across 19 national parks (Spear et al. 2011, Foxcroft et al. 2017). The SANParks estate covers an area of about 39,000 km^2 and spans eight of the nine biomes in South Africa. Using the full list of alien species recorded in SANParks by Spear et al. (2011), we extracted a subset of those alien plants we considered to be transformer species.

Transformer species were defined as the "subset of invasive plant species that change the character, condition, form, or nature of ecosystems over a substantial area relative to the extent of that ecosystem" (Richardson et al. 2000, McGeoch et al. 2006). From the overall SANParks species list we extracted those species that we considered transformers using information from four key publications, (i) Henderson (2001), declared alien weeds and invasive plants, (ii) Nel et al. (2004), a classification of invasive alien plant species in South Africa, (iii) van Wilgen et al. (2008a), a biome scale assessment of the impact of invasive alien plants, and (iv) van Wilgen et al. (2008b) prioritising species and catchments for guiding invasive alien plant management in South Africa). We also considered national legislation that regulates the management of alien and invasive plants in South Africa (CARA; Conservation of Agricultural Resources; Act 43 of 1983, as amended 2001). The criteria for designating alien plant species as transformers in our assessment were, (i) species recorded as 'transformers' or 'potential transformers' in Henderson (2001), (ii) species classified in Henderson (2001) as 'special effect weeds' AND also listed in two or more of the other publications (but in CARA only if listed as a Category 1 prohibited species) and (iii) four species in the SANParks list were considered transformer species based on the authors' personal observations in parks and supported by expert opinion. The latter resulted in the inclusion of the following species: *Austrocylindropuntia cylindrica*, *Aristolochia littoralis*, *Bryophyllum delagoense* and *Pontederia cordata*. *Pontederia cordata* was also recorded in Henderson (2001) as a 'special effects weed' and in the CARA regulations as a Category 3 invader.

This selection process resulted in a list of 139 alien plants regarded as transformer species (see Suppl. material 1: Table S1 for species list and data). By using a post hoc approach we aimed to elucidate those pathways that should be considered future management priorities for these species, and also the range and frequency of types of impacts likely to be experienced.

The potential pathways of introduction and impacts that alien plant species may have in national parks in South Africa were determined by the authors as a group, using literature (for example Mack et al. 2000, Morse et al. 2004, Randall et al. 2008, Vilà et al. 2010, Wells et al. 1986). As the classification was based on information not only from South Africa but also from other parts of the world, where data on impacts and pathways associated with species on our list are available, and it has not been proven that they actually occur in the parks under study, we term the pathways and impact categories 'potential' (see Rumlerová et al. 2016). The rationalisation of categories resulted in a list of eight locally-relevant pathways (nationally and within parks) of introduction and dispersal: rivers; ornamental plants; roads, paths, trails, tracks; contaminated construction material, equipment, soils; agriculture; clothing; food or produce; and dispersal by animals (Table 1) and 13 impacts: fire properties; geomorphology; hydrological regimes; nutrient/mineral dynamics; light; pH, salinity, alkalinity; physical structure; facilitation; alteration of successional process; competition; hybridisation; poison, allelopathy; and disruption of ecological interactions (Table 2). This was done to prevent the inclusion of pathways and impacts not

Table 1. Definition and interpretation of pathways of introduction.

Pathway	Interpretation
Rivers	Unintentional: The species is introduced by rivers (e.g. seeds that float downstream into the park).
Roads, paths, trails, tracks	Roads, paths, trails, tracks facilitate movement of the species.
Contaminated construction material, equipment, and soils	Unintentional: The species (seeds or small plants) is spread in construction material (e.g. building sand, crushed stone, gravel, bricks, timber, thatch), equipment (pumps) and soil (excluding material on transport vehicles like bulldozers or trucks).
Ornamental plants	The species is deliberately introduced as an ornamental plant by staff living in a park, or in landscaping in tourist facilities. Former farmsteads or abandoned structures incorporated into new parks may have ornamental plants associated with them.
Agriculture	The species is deliberately introduced for agriculture (small scale for staff or tourist use), or was the previous landuse in areas which now, or in the future, may be incorporated into new parks.
Clothing	Unintentional: The species is introduced on human clothing (normally seeds).
Food or produce	Unintentional: The species is introduced along with food substances brought into the park for staff, tourists, pets and animals. Note for intentional food imports the category "Agriculture" should be used.
Animal dispersed	Unintentional: The species is spread by animals (e.g. seed burs that get transported in animals' coats, birds and baboons eating fruit).

relevant to the local context. While there are many recognised pathways by which alien species are introduced, for example 32 categories listed in Hulme et al. (2008), the eight included here were deemed practical for our purposes and for management application in a protected area on a local scale. While some pathways seem counterintuitive for protected areas, all eight were deemed relevant. For example, ornamental plants are often cultivated in tourist camps and staff accommodation, or can be found at former farm houses/abandoned structures now part of a protected area. Similarly, agriculture is largely relevant for former agricultural land now incorporated into protected areas, but is also relevant where species are introduced directly adjacent to protected areas.

For each species the likelihood of being introduced by each of the eight pathways, and of having negative impacts in each of the 13 impact categories, was assessed using three primary local resources (Wells et al. 1986, Henderson 2001, Bromilow 2010), supplemented by international literature, (ISSG 2015 – Global Invasive Species Database) where the findings were deemed locally applicable by our expert judgement. We acknowledge that a species that has a diverse range of potential impacts does not necessarily equate to having the most severe impact (see Blackburn et al. 2014, Rumlerová et al. 2016). We were instead interested in quantifying the range of impacts that a species may exert on a system. This would indicate the different protected areas' objectives that may be compromised and thus the threats requiring prioritisation.

Three options were used to describe whether a species has the potential to result in an impact described by each of the 13 categories: (i) Yes – the species has been docu-

Table 2. Definition and interpretation of impact categories.

Higher category	Heading/ Impact	Interpretation
Impact on ecosystem processes and system-wide parameters	Fire properties	The species alters fire frequency, intensity or timing (of the fire regime). If species only occurs in forest, it is unlikely to impact on fire, because fire is not part of the system (No). If the species is only ruderal, it is not likely to impact on fire (No).
	Geomorphology	The species affects erosion, sedimentation processes or geo-engineers soil structure or geomorphological processes.
	Hydrological regimes	The species affects run-off and other hydrological process like flow rate, the frequency of flood events or timing and seasonality of water flow – or could change the "pattern" – physical water course.
	Nutrient/Mineral dynamics	The species alters the nutrient or mineral content of its environment (soil or water). This includes eutrophication. This can be marked yes in addition to the column "pH, salinity, alkalinity".
	Light	The species affects the amount of light filtering to layers below it (in water or sub-canopy). Yes – based on the habitat the species invades, and the structure of the plant, it is likely to affect the amount of light that reaches the layer directly below it. Unknown – it is unclear from the species structure and habitat whether light is affected. No – light not affected (e.g. species low growing terrestrial species).
	pH, salinity, alkalinity	The species affects the pH, salinity or alkalinity of the medium in/on which it occurs. This can be marked yes in addition to the column "Nutrient/Mineral dynamics". Yes – species where this has been recorded. Unknown - alleopathic species have the potential to alter pH. No – no evidence of altering pH and unlikely to do so because of life-form (e.g. vine) or other traits.
Impact on community structure	Physical structure	The species adds (or removes) a new layer to the community (e.g. tree in shrub-land, aquatic plants where no plants previously covered the water).
Impact on community composition	Facilitation	The species facilitates the invasion of other aliens. Yes – must directly facilitate the invasion or dispersal of another alien species (e.g. by providing food for the species).
	Alteration of successional process	This species alters successional processes in areas where low level disturbance is common (e.g. flood plains). Also includes species that change the disturbance regime (e.g. creation of gaps or disturbed areas).
Impact on individual indigenous species	Competition	The species competes with native species.
	Hybridization	The species can hybridise with related native species.
	Poison / allelopathy / stinging	The species may poison, sting or have allelopathic effects on other species.
Species interactions	Disruption of ecological interactions	The species disrupts native ecological interactions (including any mutualisms (e.g. seed dispersal), predator prey interactions, pollination, herbivory or other trophic interactions). Interactions include: Disruption of native seed (or fruit) dispersal due to provision of alternate food source. Effects on plant herbivore interactions by displacing food sources (e.g. unpalatable grass), breeding sites and habitat (e.g. of birds, fish and crocodiles) transformed until the species can no longer use a river. Alteration of food webs (e.g. trophic cascade). Species that only restrict movement without demonstrating disruption of an interaction were excluded.

mented to impact in this way or there is other evidence, including authors' specialist judgement, that the species will do so. (ii) No – the species does not impact in this manner or the impact is very unlikely and has never been documented for this species. (iii) Unknown – there is too little information to make a confident decision as to whether the species may impact in this manner, but this is not implausible given the biology of its taxonomic group. To be conservative, unknown records were treated as 'No' records for some analyses (detailed below). For pathways of entry, all pathways for each species could confidently be scored as 'Yes' or 'No' (i.e. no species/pathway combination was scored as 'Unknown'). In addition to the impact and pathway data we also recorded family, life-form, park invaded (Spear et al. 2011) and biome invaded (van Wilgen et al. 2008a, b).

Species were divided among authors and scored for pathways and impacts. Thereafter, a subset of species was randomly selected by category to check for consistency within, and between, categories and authors. Categories where inconsistencies were identified were systematically verified by the group for all species individually, specifically comparing entries within and between categories. The data were also checked by grouping species based on their similarity (Jaccard index) of impacts, particularly the number of impacts shared. Species that appeared to be outliers were then further examined to ensure data consistency.

Analysis

Distribution of species across life-forms, families, parks, biomes, pathways and impact categories

Species were counted across life-forms, families, pathways and impact categories, to determine the status of transformer species in SANParks. For this analysis, the aforementioned data were transformed to binary as follows: Yes – 1, No – 0, Unknown – 0.

To determine the importance of each variable we tested for significant differences between the numbers of species counted within each category. The data were expanded into unique combinations across each category, resulting in a total of 32,718 records. The variables for impacts were maintained as Yes–No–Unknown, from which combinations including Unknown records were then excluded from the analyses. Analyses were run in R 3.0.2 (R Development Core Team 2010), using the base stats library and the chi-squared contingency table and goodness-of-fit tests.

Relationship between impact and biome, park and pathway type

A Generalised Linear Model with quasi-poisson error distribution was used to examine the relationships between the count of numbers of impacts per species, with the number of pathways by which it can invade the biomes and parks in which it occurs. The analysis was performed on all 139 species, using the glm function in R to determine the relationship of the number of impact types with the number of biomes, parks and pathways per species.

Similarity in species clusters by pathways and impacts

We assessed the occurrence of groups of species with similar pathways of introduction or similar impacts to identify groups for which particular management strategies might be effective. A statistical test for non-independence of columns, using a Spearman's rank order correlation matrix was performed in R. The variables were weighted as follows for impacts and pathways: Yes – 1, No – 0, Unknown – 0.

Spearman rank correlations were conducted between all variables to exclude strongly correlated variables ($r_s > 0.60$). None of the pathway variables were highly correlated (See Suppl. material 2: Table S2: Spearman rank order correlation matrix of variables for pathways) nor were any of the impact variables (See Suppl. material 2: Table S3: Spearman rank order correlation matrix of variables for impacts).

A binary species by impact matrix, and species by pathway matrix, was constructed and the Jaccard's index calculated in Estimate S 7.51 (Colwell 2013), and used to represent the similarity of impact and pathway types between species. Cladograms were then constructed in Primer (Clarke and Gorley 2006) using group averaging. The groupings of species were examined, noting their shared impacts and pathways, mean number of impacts and pathways, and taxonomic representation in the groups.

Results

Distribution of species across life-forms, families, parks, biomes, pathways and impact categories

The transformer plant species present in parks represent 43 families, with the three most represented families being Fabaceae (20% of all the taxa assessed), Myrtaceae (9%) and Cactaceae (8%), and all other families contributing 5% or less. There were significant differences among life forms of transformer species ($\chi^2 = 118.7626$, df = 8, $P < 0.001$; Table 3), with trees (37.4%) or tree/shrubs (17.2%) over-represented and the six other life-forms less represented (See Suppl. material 2: Table S4).

There were significant differences in the number of transformer species per biome ($\chi^2 = 155.7173$, df = 7, $P < 0.001$; Table 3), with the fynbos (78% of the taxa assessed), then forest (48%) and savanna (45%), having the highest number of taxa (See Suppl. material 2: Table S5). The succulent karoo (6%) and arid savanna (9%) have the fewest transformer species recorded. In agreement with this, there were significant differences between the number of species recorded per park ($\chi^2 = 372.3872$, df = 18, $P < 0.001$), the pattern thereof largely similar to the biomes. Table Mountain National Park (hereafter Table Mountain), which is fynbos dominated, including 60% of the transformers, followed by Garden Route National Park (Garden Route), which is forest and fynbos dominated including 45%, and Kruger National Park (Kruger), a savanna protected area, including 45% of the species (See Suppl. material 2: Table S6: Total count and percentage of species per biome). Golden Gate

Table 3. Differences in numbers of transformer plant species per impact category, pathway, biome, park and life-form. (Chi-square test results for individual models), (See Figures 3, 4).

Number of:	Chi-square	df	Significance
Species per impact category	346.92	12	$P < 0.001$
Number of species per pathway type	193.61	7	$P < 0.001$
Number of species per biome	155.71	7	$P < 0.001$
Number of species per park	372.38	18	$P < 0.001$
Number of life forms per species	118.7626	8	$P < 0.001$

Highlands National Park (Golden Gate), Agulhas National Park (Agulhas), Addo Elephant National Park (Addo) and Camdeboo National Park (Camdeboo) have moderate levels of transformers, whereas the remaining 12 parks have significantly lower transformer species richness.

We found a significant difference in the numbers of species within each pathway category ($\chi^2 = 193.6135$, df = 7, $P < 0.001$; Table 3). Ornamental species (78%), rivers (63%) and animal dispersion (48%) may be considered the most important pathways of introduction and spread, with numbers of species, and thus likelihood of invasion through these pathways being higher (Figure 1). Roads, paths, trails and tracks introduce less than a half (40%) of the species assessed, while the highest of the next four pathways, agriculture, contaminated materials, clothing and food is responsible for introducing less than 29% (Figure 1) (See Suppl. material 2: Table S6: Total count and percentage of species per pathway and life form).

For impacts, there is a significant difference in the numbers of species within each impact category ($\chi^2 = 346.9231$, df = 12, $P < 0.0001$; Table 3). Nearly all 139 species are capable of direct competition with native species (Figure 2; See Suppl. material 2: Table S7: Total count and percentage of species per impact type and life form). The next most frequent types of impacts are changes to physical structure, light and then hydrological regimes. Trees and shrubs are represented in all impact categories (Figure 2).

Relationship between impact and biome, park and pathway type

There was no relationship between the number of impact types per species and the number of biomes ($P = 0.331$) or parks in which the species occurred ($P = 0.131$) (Table 4). The only significant relationship showed that species with more impacts are likely to be introduced by more pathways ($P < 0.0001$; Table 4).

Similarity in species clusters by pathways and impacts

The pathway cluster analysis separated the species into three main groups and four sub-groups (Figure 3; See Suppl. material 2: Figure S1 for detailed species names). The

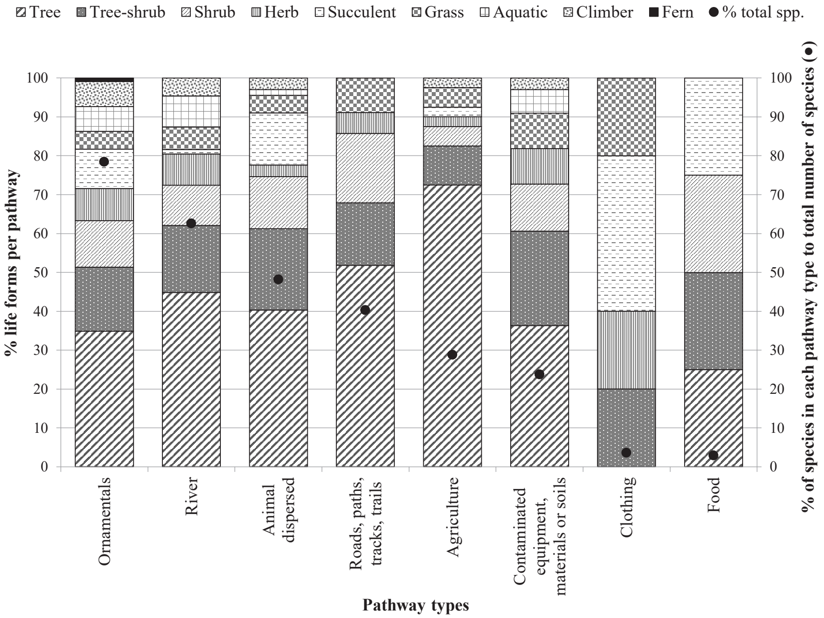

Figure 1. Percentage life forms and total percent species per pathway. Columns show the percent of each life form per pathway type, with the total number of species per pathway above each column. For example, 35% of the species that can be introduced as ornamental plants are trees, and trees make up 45% of the species that can be spread by rivers. Black dots show the total percent of species per pathway type. For example, 78% of the total species can be introduced as ornamental plants, 63% as rivers and 48% by animals.

Table 4. The relationship between number of impact types per species and number of biomes invaded, parks invaded and pathways per species. (General linear model with quassi-Poisson link function).

Term	Coefficient Estimate	Std. Error	t- value	Significance
(Intercept)	1.113	0.120	9.237	$P < 0.001$
Number of biomes per species	-0.049	0.050	-0.975	0.331
Number of parks per species	0.040	0.026	1.520	0.131
Number of pathway types per species	0.154	0.029	5.239	$P < 0.001$

first group (group a; Figure 3) consists of 45 species that are introduced by a mean of 3.8 pathways per species, predominantly roads, paths, trails and tracks (91% of the species that have this as a pathway fall in this group only), ornamentals (82%) and rivers (78%). The second group (group b; Figure 3) is a large group of 77 species that are introduced by a mean number of 2.3 pathways, which for most species includes introduction as ornamentals (94%) and via rivers (79%). For the most part, examination of clusters at the finest scale did not reveal readily interpretable patterns. Only five out

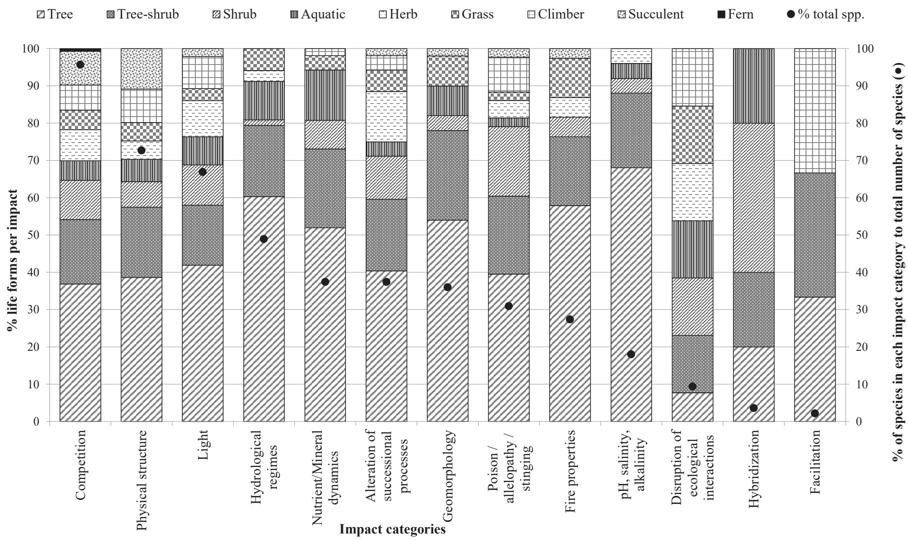

Figure 2. Percentage life forms and total percent species per impact category. Columns show the percent of life forms per each impact category, with the total number of species per impact category above each column. For example 37% of the species in the competition category are trees and 39% of the species that can impact through changes to physical structure are trees. The black dots show the percent of species in each impact category of the total species list. For example, 96% of the species could impact through direct competition, while 73% could impact through changing the physical structure.

of the 13 *Acacia* species comprised a single cluster (group h; Figure 3), which, falling in sub-group (d) indicates their ability to disperse via four pathways.

In the cluster analysis of impact categories, three main groups were observed (Figure 4; See Suppl. material 2: Figure S2 for detailed species names). The first group of 12 species (group a; Figure 4) had fewer impacts (mean of 1.63) with the majority of species impacting via competition (67%). The second group contains 97 species with a mean number of 5.63 impacts, representing all 13 impacts. Competition (98%) and physical structure (93%) were the most important. The third group (group c; Figure 4) includes 30 species, which are characterised by a mean number of 3.67 impacts per species. All these species include competition (100%) and 93.3 % of the species impact through poison or allelopathy.

In contrast to the cladogram for pathways, there were four instances where related species clustered together based on the similarities of their impacts. All four *Opuntia* and two *Cylindropuntia* species (group h; Figure 4) were clustered, as were all six *Eucalyptus* species (group I; Figure 4), all seven *Pinus* species (group j; Figure 4) and all 13 *Acacia* species (group k; Figure 4). The cacti include competition and physical structure as the most important impacts. The *Eucalyptus*, *Pinus* and *Acacia* species include both competition and physical structure as key impacts, but also fell into the only sub-group in which fire was important.

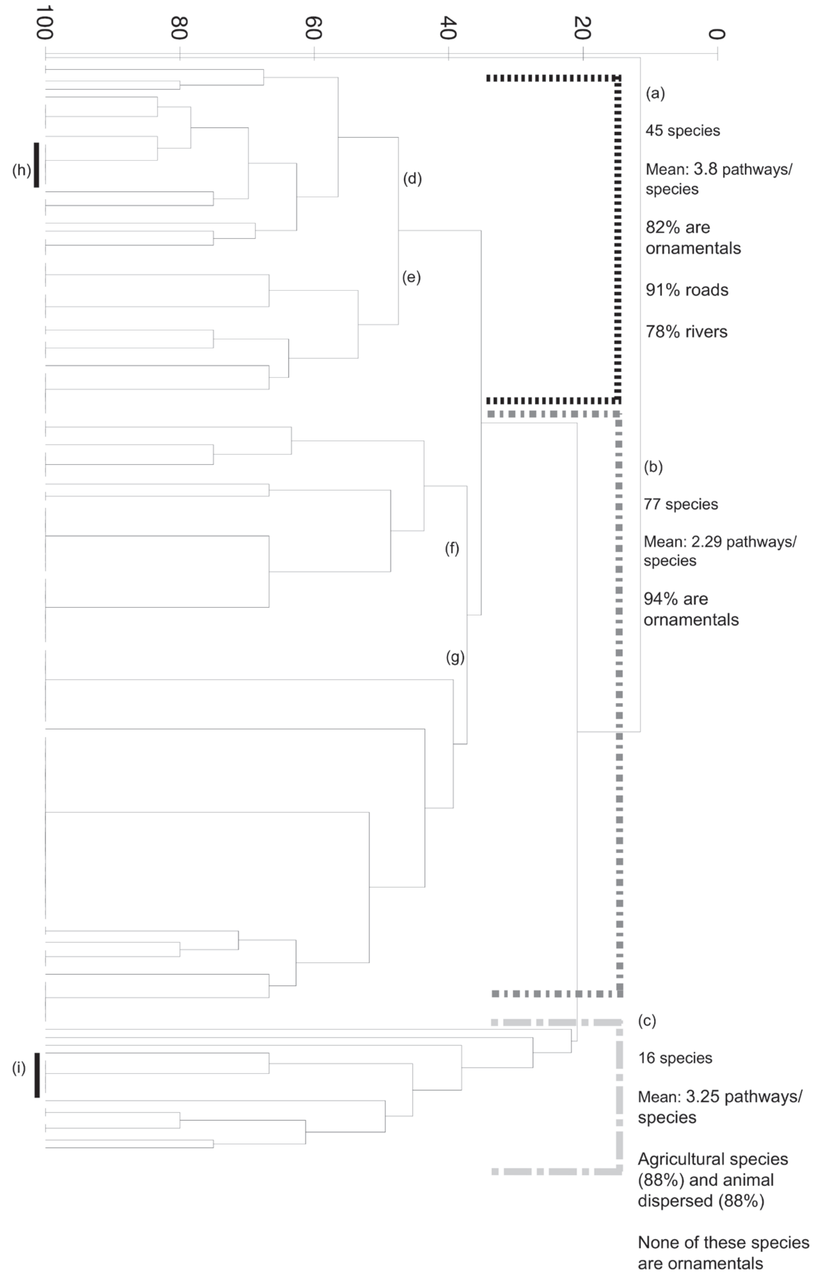

Figure 3. Cladogram of plant introduction pathways, based on similarities of pathways. Mean number and type of pathways have been calculated per clade (Groups **a–c**). Sub-groups **d** include 25 species (Mean: 4.5 pathways/species; 100% contaminants; 92% rivers; 84% roads; 80% ornamentals) **e** include 20 species (Mean: 2.9 pathways/species; 100% roads; 85% ornamentals) **f** include 29 species (Mean: 2.5 pathways/ species; 96% ornamentals; 90% animals) **g** include 48 species (Mean: 2.1 pathways/species; 91% ornamentals). The vertical black bars indicate clustering of species, whereas all other species are scattered across the groups **h** *Acacia podalyriifolia*, *A. baileyana*, *A. elata*, *A. implexa*, *A. longifolia* **i** *Pinus pinaster*, *P. radiata*, *P. roxburghii*, *P. taeda*, *P. halepensis*, *P. patula.*

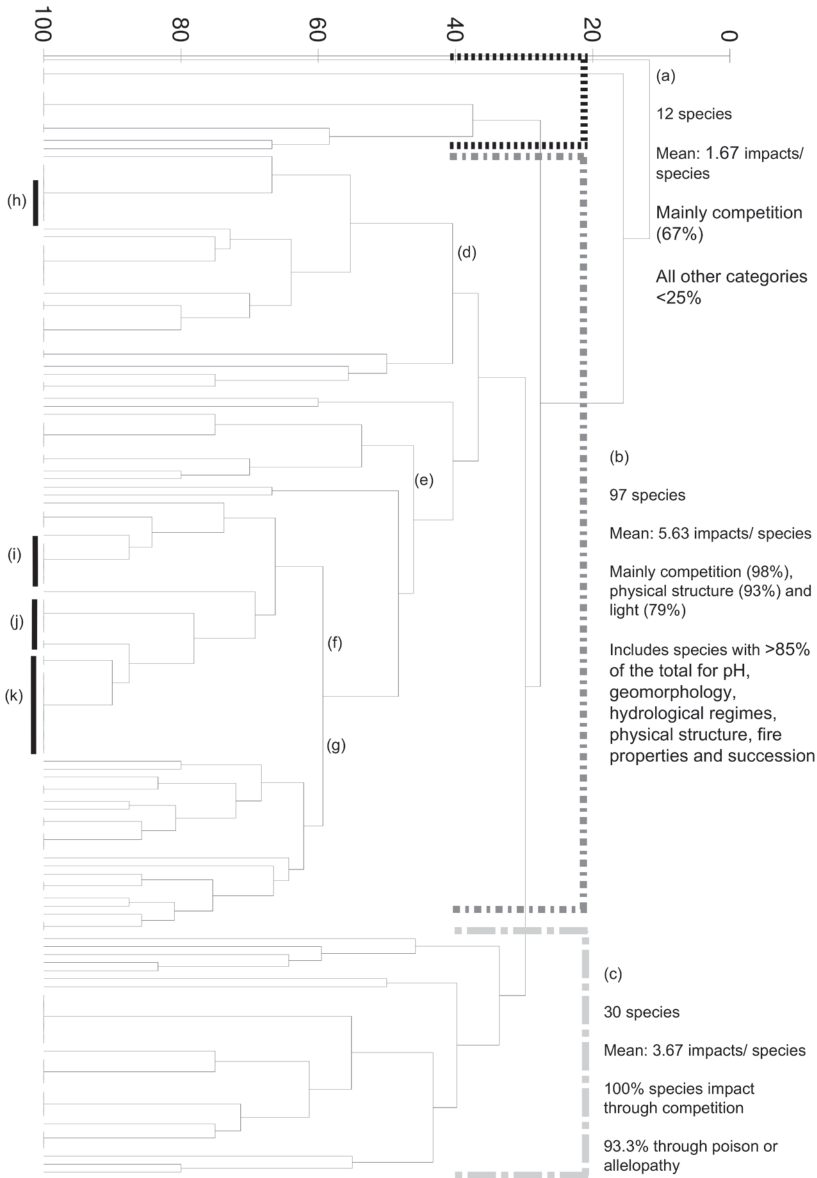

Figure 4. Cladogram of plant impacts, based on similarities of impact types. Mean number and type of impacts have been calculated per clade (Groups **a–c**). Sub-groups include **d** 24 species (Mean: 3 impacts/species; 100% competition; physical structure 100%) **e** 11 species (Mean: 4.6 impacts/species; 100% competition; physical structure 100%; 82% hydrological) **f** 32 species (Mean: 7.9 impacts/species; competition, physical structure, light, hydrology, fire >90%) **g** 22 species (Mean: 6.4 impacts/species; competition, physical structure, light, hydrology >90%). The vertical black bars indicate clustering of species, whereas all other species are scattered across the groups **h** *Cereus jamacaru*, *Echinopsis spachiana*, *Opuntia aurantiaca*, *O. ficus-indica*, *O. humifusa*, *Cylindropuntia imbricata*, *C. fulgida*, *Opuntia stricta* **i** *Eucalyptus cladocalyx*, *E. lehmannii*, *E. sideroxylon*, *E. camaldulensis*, *E. diversicolor* **j** *Pinus radiata*, *P. roxburghii*, *P. taeda*, *P. halepensis*, *P. patula*, *P. canariensis*, *P. pinaster* **k** *Acacia dealbata*, *A. mearnsii*, *A. melanoxylon*, *A. paradoxa*, *A. podalyriifolia*, *A. pycnantha*, *A. saligna*, *A. baileyana*, *A. cyclops*, *A. decurrens*, *A. elata*, *A. implexa*, *A. longifolia*.

Discussion

The role of pathways of invasion for prioritising management actions

The two most important pathways of invasion identified for transformer species into national parks included use as ornamental species and rivers. An additional two pathways appear to play a role as vectors, although to a lesser extent, including dispersal by animals and along roads, paths, tracks and trails. The results from the analyses all point to the high likelihood that many of the species currently in SANParks (~80%) were introduced for ornamentation. This can be illustrated in two parks, Kruger and Table Mountain. Kruger has a long history of plant introductions and the control of ornamental plants was first recommended in 1935 (Joubert 1986). However, by 2003 more than 250 ornamental plant species were recorded in Kruger (Foxcroft et al. 2008), including 35% of the species in our list. Work by Spear et al. (2013) showed human population density surrounding a park to be a significant driver of invasion into a park. Similarly, areas with high levels of natural vegetation along the boundary of Kruger proved to be a filter to plant invasions into the park (Foxcroft et al. 2011). The use of ornamental plants at the urban-protected area interface has been shown to increase the threat to urban protected areas such as Table Mountain (Alston and Richardson 2006). Many ornamentals appear to have few other introduction pathways, suggesting that if these species were removed from ornamental use at least some species would potentially be prevented from invading in future. Ornamental species potentially remain one of the easier pathways to manage within protected areas using, for example, policy guidelines (e.g. in Kruger, Foxcroft et al. 2015) and incentive schemes to replace alien species with native species occurring within parks and potentially those in close proximity. However, propagule pressure from outside the park is harder to control. For many of the ornamental species, rivers also form important invasion pathways, necessitating working with the nursery and landscaping industry and promoting initiatives to plant indigenous alternatives outside parks and increasing surveillance in riparian areas.

Rivers have been widely acknowledged as key dispersal vectors for invasion (Richardson et al. 2007, Esler et al. 2008, Naiman and Décamps 1997, van Wilgen et al. 2007, Jarošík et al. 2011) and more than 60% of the species in our list can disperse along rivers. Propagules transported by water flow can be widely dispersed during floods, and riparian zones and rivers banks provide highly suitable habitat (Alpert et al. 2000). Surveillance activities along rivers should be flagged as a priority area to detect new species and changes in distribution (van Wilgen et al. 2007, Forsyth et al. 2012). Trees and tree-shrubs, which are likely to be more conspicuous and easier to detect, comprise only just over half of the list, suggesting that increased effort needs to be made to detect less visible species.

Although animals are widely considered to be major dispersers of invasive plants (e.g. Vavra et al. 2007, Guerrero and Tye 2011, Kueffer et al. 2009; Oatley 1984, Gosper et al. 2005), we found only half of the species in SANParks may disperse in this manner. This is surprising as most parks have native vertebrates that could utilise alien plants. There are notable examples, however, where animals form an important dispersal mechanism for species introduced via other pathways into a park. For example, in Kruger *Opuntia stricta* was introduced as an ornamental plant but due to baboons and elephants utilising the fruit it became widely invasive (Foxcroft and Rejmánek 2007).

In contrast with work done in a number of studies (e.g. Pauchard and Alaback 2004, Stohlgren et al. 2013, Lonsdale and Lane 1994, Lonsdale 1999, Tyser and Worley 1992, Gelbard and Belnap 2003), we found roads and tracks to be surprisingly less frequently listed (40% of the species). As most parks have large road networks, tracks and pathways, whether for tourism or management purposes, the comparatively lower importance of this pathway is fortunate. However, there are important examples of this pathway such as alien species found along hiking and cycling trails in Table Mountain (Bouchard et al. 2015), as well as the fact that Table Mountain is an urban park within the city of Cape Town, the rapid spread of *Parthenium hysterophorus* along roadsides leading there and in Kruger (Foxcroft et al. 2009) and *Pennisetum setaceum* in Camdeboo (Masubelele et al. 2009), which is also partly an urban park. For management purposes, sections of path can be delineated for increased surveillance and fortuitously, populations confined to roadsides, should be comparatively easier to control than other pathways.

Assessing the transformer species richness per park and biome provides some insights into the potential invasibility of an area. For example, Kruger includes about 350 alien plant species, which is about 100 alien plant species more than in Table Mountain (~240) (Spear et al. 2013). However, less than 20% of the species in Kruger are transformer plants and more than a third of the species in Table Mountain and Garden Route are transformers. Moreover, the high endemism in the Fynbos biome (Rebelo et al. 2011) and high levels of habitat loss highlights that Table Mountain should be a priority for alien species management. Garden Route, containing both fynbos and forest, should likewise be considered a high management priority. Conversely, in the arid regions, parks such as Kalahari Gemsbok, Richtersveld and Augrabies Falls National Parks are less likely to become invaded by a large suite of alien plant species, of which most are likely to be restricted to rivers and drainage lines. This does not, however, indicate immunity from other invasions. Ornamental species, for example from the Cactaceae, which are introduced and nurtured in gardens could escape once established (Novoa et al. 2015). Implementing policy to prohibit the use of ornamental species in the parks therefore provides an opportunity for ongoing prevention and thereby further minimising the already low diversity of invasions in these arid parks. Species such as *Prosopis* spp., which are river dispersed, are highly likely to remain problematic in arid areas and the importance of the impact on hydrology, especially ground water (Dzikiti et al. 2017) highlights that this species should remain a priority.

Additional support for prioritising pathways may be gained from associations or shared traits of species that clustered together, while for some groups it is clear that prioritising one or even a few pathways will not be enough to curb spread and integrated approaches will be required. For example, all *Acacia* species share four of the eight pathways, with five of the 13 species sharing exactly the same pathways. These clusters together with the large body of work on *Acacia* (Richardson et al. 2011, Wilson et al. 2011) allow broader generalisations to be inferred for this group. Similarly, six of the seven *Pinus* spp. were clustered and based on current knowledge (e.g. Richardson 2006), potential pathways for other *Pinus* spp. may be similar.

Assessing the potential impacts by alien species

That nearly all transformer species compete directly with native species is not an entirely unexpected result. More importantly, however, a large proportion (~70%) of the species showed the potential to impact in at least four additional ways. This most frequently included impacts such as altering hydrological regimes, changing light properties of invaded habitats, changing the physical structure of invaded areas, fire properties and succession. At a higher level in our categorisation these impacts were included as community structure, community composition and ecosystem level processes. These combined impacts can lead to cascading effects which are less easy, if at all possible, to reengineer (Meiners and Pickett 2013). Legacy effects can persist even after clearing has taken place (Larious and Sudding 2013) and can influence the ability of a system to recover following control efforts and whether additional interventions are required.

Four of the most represented naturalised genera globally were recorded in our list (Pyšek et al. 2017), and include some of the most frequently listed impacts. The *Opuntia* and *Cylindropuntia* spp., *Eucalyptus* spp., *Pinus* spp. and *Acacia* spp. each formed clusters of similar impacts. Excluding direct competition, physical structure was listed as the most important impact for the Cactaceae. Due to the dominance of trees and tree-shrubs in the transformer group, these species made up about half of the direct competition category and 40% of the species that can potentially change physical structure. These include the *Eucalyptus*, *Pinus* and *Acacia* species, but for these species specifically, impacts also included light, hydrology and fire. For example, species in the Fabaceae can significantly increase biomass and intensity of fires (van Wilgen and Richardson 1985), compounding long-term soil erosion (Scott et al. 1998) and other ecosystem level impacts on biogeochemistry (Yelenik et al. 2004). Therefore these species, in particular, are important and should be prioritised. In addition, groups of similar species may be advantageous in that similar management actions may be possible across the species.

Relationships between pathways and impacts

By assessing each species against the eight pathway and 13 impact categories, we aimed to determine a relative risk profile for each species that could assist in determining the threat that the species posed to a protected area. The significant relationship between pathways and impacts indicates that the more pathways a species can use to disperse, the higher the likelihood that the species will become problematic.

For protected areas in our study, a species introduced by multiple pathways can be expected to be distributed over a larger area and should be given a higher priority. For example, when spreading along rivers, riparian vegetation may be displaced, causing substantial changes to the geomorphology, vegetation and community structure and composition (Hejda et al. 2009), species communities and river bank collapse, while simultaneous spread across the landscape more broadly (e.g. grass or shrublands to alien tree dominated systems) can alter ecosystem processes (Raizada et al. 2008, Martin et al. 2009), fire regimes (e.g. Table Mountain, Forsyth and van Wilgen 2008, and *Andropogon gayanus* in Kakadu National Park in northern Australia, Rossiter et al. 2003), hydrology and nutrient cycling/biogeochemistry (e.g. Carbon-Nitrogen-water-leaf litter interactions, Ehrenfeld 2003).

Conclusions

Managers need reliable evidence on which to base their decisions about the location and nature of the species to be prioritised for management. These decisions often have substantial financial commitments with long-term ramifications. The ability to forecast which species, and the number or kinds of impacts they may have, can support decision making for different contexts. The correlation between the number of pathways and impacts per species highlights species of concern due to their ability to reach different habitats more widely. Implementing measures to curtail invasions along pathways that can be managed by implementing suitable policies (e.g. ornamental plants), or structured monitoring (e.g. along roadsides, trails and tracks), and combined with intensive surveillance (e.g. along rivers), will be important for a large proportion of the species.

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References

Alston KP, Richardson DM (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation 132: 183–198. https://doi.org/10.1016/j.biocon.2006.03.023

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 52–66. https://doi.org/10.1078/1433-8319-00004

Bacher S, Blackburn TM, Essl F, Genovesi P, Heikkilä J, Jeschke JM, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul W-C, Scalera R, Vilà M, Wilson JRU, Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). Methods in Ecology and Evolution 9: 159–168. https://doi.org/10.1111/2041-210X.12844

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12(5): e1001850. https://doi.org/10.1371/journal.pbio.1001850

Bouchard EH, Little LE, Miller CML, Rundell SM, Vlodaver EM, Maciejewski K (2015) Undeclared baggage: Do tourists act as vectors for seed dispersal in fynbos protected areas? Koedoe 57(1): 1–9. https://doi.org/10.4102/koedoe.v57i1.1323

Bromilow C (2010) Problem Plants and Alien Weeds of South Africa. Briza Publications, Pretoria, 300 pp.

Bruner AG, Gullison RE, Balmford A (2004) Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. Bioscience 54: 1119–1126. https://doi.org/10.1641/0006-3568(2004)054[1119:FCASOM]2.0.CO;2

Carey C, Dudley N, Stolton S (2000) Threats to Protected Areas. Squandering paradise? The Importance and Vulnerability of the World's Protected Areas. World Wide Fund for Nature International, Gland, 231 pp.

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, 192 pp.

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application. http://purl.oclc.org/estimates

Cook CN, Hockings M, Carter R (2010) Conservation in the dark? The information used to support management decisions. Frontiers in Ecology and the Environment 8: 181–186. https://doi.org/10.1890/090020

Dawson W, Burslem DFRP, Hulme PE (2009) The suitability of the Australian weed risk assessment as a conservation tool to identify invasive plant threats in East African rainforests. Biological Conservation 142: 1018–1024. https://doi.org/10.1016/j.biocon.2009.01.013

DeFries R, Hansen A, Newton AC, Hansen MC (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. Ecological Applications 15: 19–26. https://doi.org/10.1890/03-5258

Dixon JA, Sherman PB (1991) Economics of protected areas. Ambio 20: 68–74. https://www.jstor.org/stable/4313779

Dzikiti S, Ntshidi Z, Le Maitre DC, Bugan RDH, Mazvimavi D, Schachtschneider K, Nebojsa J, Pienaar HH (2017) Assessing water use by *Prosopis* invasions and *Vachellia karroo* trees: Implications for groundwater recovery following alien plant removal in an arid catchment in South Africa. Forest Ecology and Management 398: 153–163. https://doi.org/10.1016/j.foreco.2017.05.009

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503–523. https://doi.org/10.1007/s10021-002-0151-3

Esler KJ, Holmes PM, Richardson DM, Witkowski ETF (2008) Riparian vegetation management in landscapes invaded by alien plants: Insights from South Africa. South African Journal of Botany 74: 397–400. https://doi.org/10.1016/j.sajb.2008.01.168

Essl F, Bacher S, Blackburn TM, Booy O, Brundu G, Brunel S, Cardoso AC, Eschen R, Gallardo B, Galil B, García-Berthou E, Genovesi P, Groom Q, Harrower C, Hulme PE, Katsanevakis S, Kenis M, Kühn I, Kumschick S, Martinou AF, Nentwig W, O'Flynn C, Pagad S, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roques A, Roy HE, Scalera R, Schindler S, Seebens H, Vanderhoeven S, Vilà M, Wilson JRU, Zenetos A, Jeschke JM (2015) Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769–782. https://doi.org/10.1093/biosci/biv082

Evans MC, Possingham HP, Wilson KA (2011) What to do in the face of multiple threats? Incorporating dependencies within a return on investment framework for conservation. Diversity and Distributions 17: 437–450. https://doi.org/10.1111/j.1472-4642.2011.00747.x

Forsyth GG, Le Maitre DC, O'Farrell PJ, van Wilgen BW (2012) The prioritisation of invasive alien plant control projects using a multi-criteria decision model informed by stakeholder input and spatial data. Journal of Environmental Management 103: 51–57. https://doi.org/10.1016/j.jenvman.2012.01.034

Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (2013) Plant Invasions in Protected Areas. Patterns, Problems and Challenges. Springer, Dordrecht, 656 pp. https://doi.org/10.1007/978-94-007-7750-7

Foxcroft LC, Pyšek P, Richardson DM, Genovesi P, MacFadyen S (2017) Plant invasion science in protected areas: progress and priorities. Biological Invasions 19: 1353–1378. https://doi.org/10.1007/s10530-016-1367-z

Foxcroft LC, Jarošík V, Pyšek P, Richardson DM, Rouget M (2011) Protected-area boundaries as filters of plant invasions. Conservation Biology 25: 400–405. https://doi.org/10.1111/j.1523-1739.2010.01617.x

Foxcroft LC, Rejmánek M (2007) What helps *Opuntia stricta* invade Kruger National Park: baboons or elephants? Applied Vegetation Science 10: 265–270. https://doi.org/10.1111/j.1654-109X.2007.tb00525.x

Foxcroft LC, Richardson DM, Rouget M, MacFadyen S (2009) Patterns of alien plant distribution at multiple spatial scales in a large national park: Implications for ecology, management and monitoring. Diversity and Distributions 15: 367–378. https://doi.org/10.1111/j.1472-4642.2008.00544.x

Foxcroft LC, Richardson DM, Wilson JRU (2008) Ornamental plants as invasive aliens: problems and solutions in Kruger National Park, South Africa. Environmental Management 41: 32–51. https://doi.org/10.1007/s00267-007-9027-9

Foxcroft LC, Van Wilgen NJ, Baard JA, Cole NS (2017) Biological invasions in South African National Parks. Bothalia 47(2): a2158. https://doi.org/10.4102/abc.v47i2.2158

Foxcroft LC, Zambatis G, Zambatis N, Hofmeyr M, Petersen TA, Khoza E (2015) Protocol for the management of ornamental alien plants and landscaping in all developed areas of the Kruger National Park. Reference Number: 16/Pr- KNP Management. Conservation Services, Kruger National Park, South African National Parks.

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17: 420–432. https://doi.org/10.1046/j.1523-1739.2003.01408.x

Geldmann J, Barnes M, Coad L, Craigie ID, Hockings M, Burgess ND (2013) Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation 161: 230–238. https://doi.org/10.1016/j.biocon.2013.02.018

Gosper CR, Stansbury CD, Vivian-Smith G (2005) Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. Diversity and Distributions 11: 549–558. https://doi.org/10.1111/j.1366-9516.2005.00195.x

Guerrero AM, Tye A (2011) Native and introduced birds of Galapagos as dispersers of native and introduced plants. Ornitología Neotropical 22: 207–217.

Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97: 393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Henderson L (2001) Alien Weeds and Invasive Plants. Plant Protection Research Institute Handbook No.12, Plant Protection Research Institute, Agricultural Research Council, Pretoria, 300 pp.

Hulme PE (2006) Beyond control: Wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835–847. https://doi.org/10.1111/j.1365-2664.2006.01227.x

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46: 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Hulme PE (2012) Weed risk assessment: A way forward or a waste of time? Journal of Applied Ecology 49: 10–19. https://doi.org/10.1111/j.1365-2664.2011.02069.x

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: A framework for integrating pathways into policy. Journal of Applied Ecology 45: 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Hulme PE, Pyšek P, Pergl J, Jarošík V, Schaffner U, Vila M (2013) Greater focus needed on alien plant impacts in protected areas. Conservation Letters 7: 459–466. https://doi.org/10.1111/conl.12061

ISSG [Invasive Species Specialist Group] (2015) The Global Invasive Species Database. Version 2015.1 http://www.iucngisd.org/gisd/

Jarošík V, Pyšek P, Foxcroft LC, Richardson DM, Rouget M, MacFadyen S (2011) Predicting incursion of plant invaders into Kruger National Park, South Africa: The interplay of general drivers and species-specific factors. PLoS ONE 6: e28711. https://doi.org/10.1371/journal.pone.0028711

Joubert SCJ (1986) Master plan for the management of Kruger National Park. South African National Parks (formerly National Parks Board), Skukuza.

Koh LP, Gardner TA (2010) Conservation in human-modified landscapes. In: Sodhi NS, Ehrlich PR (Eds) Conservation Biology for All. Oxford University Press, Oxford, 236–258. https://doi.org/10.1093/acprof:oso/9780199554232.003.0014

Kueffer C, Kronauer L, Edwards PJ (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. Oikos 118: 1327–1334. https://doi.org/10.1111/j.1600-0706.2009.17185.x

Larious L, Sudding KN (2013) Restoration within protected areas: When and how to intervene to manage plant invasions? In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) Plant Invasions in Protected Areas. Patterns, problems and challenges. Springer, Dordrecht, 599–618. https://doi.org/10.1007/978-94-007-7750-7_27

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B 269: 2407–2413. https://doi.org/10.1098/rspb.2002.2179

Leung B, Roura-Pascual N, Bacher S, Heikkilä J, Brotons L, Burgman MA, Dehnen-Schmutz K, Essl F, Hulme PE, Richardson DM, Sol D, Vilà M, Rejmánek M (2012) TEASIng apart alien species risk assessments: A framework for best practices. Ecology Letters 15: 1475–1493. https://doi.org/10.1111/ele.12003

Lonsdale WM (1999) Global patterns of plant invasions, and the concept of invasibility. Ecology 80: 1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

Lonsdale WM, Lane AM (1994) Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. Biological Conservation 69: 277–283. https://doi.org/10.1016/0006-3207(94)90427-8

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710. https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Martin MR, Tipping PW, Sickman LO (2009) Invasion by an exotic tree alters above and belowground ecosystem components. Biological Invasions 11: 1883–1894. https://doi.org/10.1007/s10530-008-9366-3

Masubelele ML, Foxcroft LC, Milton SJ (2009) Alien plant species list and distribution for Camdeboo National Park, South Africa. Koedoe 51(1): 1–10. https://doi.org/10.4102/koedoe.v51i1.515

McGeoch MA, Chown SL, Kalwij JM (2006) A global indicator for biological invasion. Conservation Biology 20: 1635–1646. https://doi.org/10.1111/j.1523-1739.2006.00579.x

McGeoch MA, Genovesi P, Bellingham PJ, Costello MJ, McGrannachan C, Sheppard A (2016) Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biological Invasions 18: 299–314. https://doi.org/10.1007/s10530-015-1013-1

McGeoch MM, Shongwe N, Dopolo M, Freitag-Ronaldson S, Fisher R, Bester E, Kruger N, Moses M, Holness S, Oosthuizen A, Smit IPJ, Seydack A, Durrheim G, Hofmeyr M, Hanekom N, Moolman L, Buss P, Joubert J, Goosen L, Ferreira S, Randall R, Kraaij T, Govender N, Kruger J, Williams C, Foxcroft LC, Moore K, Smith K, Zimmerman D, Baard J, Mamfengu P, Russell I, Biggs HC, Govender D, Tally-Palmer C (2009) Global environmental change in South African National Parks. Report on the outcome of the global environmental change workshop, conservation services division imbizo, Pretoria 2008. South African National Parks Scientific Report 03/2009, 1–34.

Meiners SJ, Pickett STA (2013) Plant invasions in protected landscapes: Exception or Expectation? In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) Plant Invasions in Protected Areas. Patterns, Problems and Challenges. Springer, Dordrecht, 43–60. https://doi.org/10.1007/978-94-007-7750-7_3

Morse LE, Randall JM, Benton N, Hiebert R, Lu S (2004) An invasive species assessment protocol: Evaluating non-native plants for their impact on biodiversity. Version 1. NatureServe, Arlington, Virginia, 40 pp.

Naiman RJ, Décamps H (1997) The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics 28: 621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621

Nel JL, Richardson DM, Rouget M, Mgidi TN, Mdzeke N, Le Maitre DC, van Wilgen BW, Schonegevel L, Henderson L, Neser S (2004) A proposed classification of invasive alien plant species in South Africa: Towards prioritizing species and areas for management action. South African Journal of Science 100: 53–64. http://hdl.handle.net/10520/EJC96213

Nentwig W, Bacher S, Pyšek P, Vilà M, Kumschick S (2016) The Generic Impact Scoring System (GISS): A standardized tool to quantify the impacts of alien species. Environmental Monitoring and Assessment 188: 315. https://doi.org/10.1007/s10661-016-5321-4

Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilà M (2018) More than "100 worst" alien species in Europe. Biological Invasions 20: 1611–1621. https://doi.org/10.1007/s10530-017-1651-6

Novoa A, Le Roux JJ, Robertson MP, Wilson JRU, Richardson DM (2015) Introduced and invasive cactus species: A global review. AoB PLANTS 7: plu078. https://doi.org/10.1093/aobpla/plu078

Oatley TB (1984) Exploitation of a new niche by the rameron pigeon *Columba arquatrix* in Natal. In: Ledger J (Ed.) Proceedings of the Fifth Pan-African Ornithological Congress, Lilongwe (Malawi) 1980. Southern African Ornithological Society, Johannesburg, 323–330.

Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. Conservation Biology 18: 238–248. https://doi.org/10.1111/j.1523-1739.2004.00300.x

Pergl J, Sádlo J, Petrusek A, Laštůvka Z, Musil J, Perglová I, Šanda R, Šefrová H, Šíma J, Vohralík V, Pyšek P (2016) Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. NeoBiota 28: 1–37. https://doi.org/10.3897/neobiota.28.4824

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. Global Change Biology 18: 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

Pyšek P, Pergl J, Essl F, Lenzner B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castańo N, Chacón E, Chatelain C, Dullinger S, Ebel AL, Figueiredo E, Fuentes N, Genovesi P, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Maurel N, Meerman J, Morozova O, Moser D, Nickrent D, Nowak PM, Pagad S, Patzelt A, Pelser PB, Seebens H, Shu W, Thomas J, Velayos M, Weber E, Wieringa JJ, Baptiste MP, van Kleunen M (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia 89: 203–274. https://doi.org/10.23855/preslia.2017.203

Raizada P, Raghubanshi AS, Singh JS (2008) Impact of invasive alien plant species on soil processes: A review. Proceedings of the National Academy of Science India B 78: 288–98.

Randall JM, Morse LE, Benton N, Hiebert R, Lu S, Killeffer T (2008) The invasive species assessment protocol: A tool for creating regional and national lists of invasive nonnative plants that negatively impact biodiversity. Invasive Plant Science and Management 1: 36–49. https://doi.org/10.1614/IPSM-07-020.1

Rebelo AG, Freitag S, Cheney C, McGeoch MA (2011) Prioritising species of special concern for monitoring in Table Mountain National Park: The challenge of a species-rich, threatened ecosystem. Koedoe 53(2): 1–14. https://doi.org/10.4102/koedoe.v53i2.1019

Richardson DM (2006) *Pinus*: A model group for unlocking the secrets of alien plant invasions? Preslia 78: 375–388.

Richardson DM, Carruthers J, Hui C, Impson FA, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU (2011) Human-mediated introductions of Australian acacias – A global experiment in biogeography. Diversity and Distributions 17: 771–787. https://doi.org/10.1111/j.1472-4642.2011.00824.x

Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007) Riparian vegetation: Degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13: 126–139. https://doi.org/10.1111/j.1366-9516.2006.00314.x

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity and Distributions 6: 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Rossiter NA, Setterfield SA, Douglas MM, Hutley LB (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions 9: 169–176. https://doi.org/10.1046/j.1472-4642.2003.00020.x

Rumlerová Z, Vilà M, Pergl J, Nentwig W, Pyšek P (2016) Scoring environmental and socioeconomic impacts of alien plants invasive in Europe. Biological Invasions 18: 3697–3711. https://doi.org/10.1007/s10530-016-1259-2

Scott DF, Versfeld DB, Lesch W (1998) Erosion and sediment yields in relation to afforestation and fire in the mountains of the Western Cape Province, South Africa. South African Geographical Journal 80: 52–59. https://doi.org/10.1080/03736245.1998.9713644

Simberloff D (2013) Eradication: Pipe dream or real option? In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) Plant Invasions in Protected Areas: Patterns, Problems and Challenges. Springer, Dordrecht, 549–559. https://doi.org/10.1007/978-94-007-7750-7_25

Spear D, Foxcroft LC, Bezuidenhout H, McGeoch MA (2013) Human population density explains alien species richness in protected areas. Biological Conservation 159: 137–147. https://doi.org/10.1016/j.biocon.2012.11.022

Spear D, McGeoch MA, Foxcroft LC, Bezuidenhout H (2011) Alien species in South Africa's National Parks (SANParks). Koedoe 53(1): 1–4. https://doi.org/10.4102/koedoe.v53i1.1032

Sutherland WJ, Spielgelhalter D, Burgman MA (2013) Twenty tips for interpreting scientific claims. Nature 503: 335–337. https://doi.org/10.1038/503335a

Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology 6: 253–262. https://doi.org/10.1046/j.1523-1739.1992.620253.x

Stohlgren TJ, Loope LL, Makarick LJ (2013) Invasive plants in the United States National Parks. In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) Plant Invasions in Protected Areas. Patterns, Problems and Challenges. Springer, Dordrecht, 267–283. https://doi.org/10.1007/978-94-007-7750-7_13

van Wilgen BW, Fill JM, Baard J, Cheney C, Forsyth AT, Kraaij T (2016) Historical costs and projected future scenarios for the management of invasive alien plants in protected areas in the Cape Floristic Region. Biological Conservation 200: 168–177. https://doi.org/10.1016/j.biocon.2016.06.008

van Wilgen BW, Nel J, Rouget M (2007) Invasive alien plants and South African rivers, a proposed approach to the prioritization of control operations. Freshwater Biology 52: 711–723. https://doi.org/10.1111/j.1365-2427.2006.01711.x

van Wilgen BW, Forsyth GG, Le Maitre DC (2008a) The prioritization of species and primary catchments for the purposes of guiding invasive alien plant control operations in the terrestrial biomes of South Africa. Council for Scientific and Industrial Research, Stellenbosch, 1–51. [Report number: CSIR/NRE/ECO/ER/2008/0070/C]

van Wilgen BW, Reyers B, Le Maitre DC, Richardson DM, Schonegevel L (2008b) A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. Journal of Environmental Management 89: 336–349. https://doi.org/10.1016/j.jenvman.2007.06.015

van Wilgen BW, Richardson DM (1985) The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrubland: A simulation study. Journal of Applied Ecology 22: 955–966. https://doi.org/10.2307/2403243

Vavra M, Parks CG, Wisdom MJ (2007) Biodiversity, exotic plant species, and herbivory: The good, the bad, and the ungulate. Forest Ecology and Management 246: 66–72. https://doi.org/10.1016/j.foreco.2007.03.051

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8: 135–144. https://doi.org/10.1890/080083

Wells MJ, Balsinhas AA, Joffee H, Engelbrecht VM, Harding G, Stirton CH (1986) A catalogue of problem plants in southern Africa – Memoirs of the botanical survey of South Africa No. 53. Botanical Research Institute, Pretoria, 1–658.

Wilson JRU, Gairifo C, Gibson MR, Arianoutsou M, Bakar BB, Baret S, Celesti-Grapow L, DiTomaso JM, Dufour-Dror J-M, Kueffer C, Kull CA, Hoffmann JH, Impson FAC, Loope LL, Marchante E, Marchante H, Moore JL, Murphy DJ, Tassin J, Witt A, Zenni RD, Richardson DM (2011) Risk assessment, eradication, and biological control: Global efforts to limit Australian acacia invasions. Diversity and Distributions 17: 1030–1046. https://doi.org/10.1111/j.1472-4642.2011.00815.x

Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African Fynbos. Restoration Ecology 12: 44–51. https://doi.org/10.1111/j.1061-2971.2004.00289.x

Supplementary material 1

Data for species and their pathways and impacts per category

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Data type: species data

Link: https://doi.org/10.3897/neobiota.43.29644.suppl1

Supplementary material 2

Assessing the association between pathways of alien plant invaders and their impacts in protected area

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Data type: measurement

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